Phytoplankton productivity across Moreton Bay, Queensland, Australia: the impact of water quality, light and nutrients on spatial patterns

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ABSTRACT

Phytoplankton productivity and the factors that regulate it were studied across Moreton Bay (27°S, 153°E), a large embayment on the subtropical East Australian coast. Depth profiles of salinity, temperature, pH, turbidity and dissolved oxygen were measured at 73 sites across the Bay. Our measurements showed a general landward to seaward trend in salinity, turbidity and dissolved oxygen profiles, so we have used a representative 20 km transect extending from the mouth of the Brisbane River to the Moreton Bay Research Station at Dunwich on North Stradbroke Island to present our findings. Phytoplankton pigment concentrations were measured at all 73 sites and were generally highest in areas with lower water clarity (Secchi depths < 3.25 m), suggesting nutrients (often associated with turbid waters) rather than light may be determining phytoplankton distributions in Moreton Bay. Based on traditional light/dark bottle experiments undertaken on samples collected at fourteen sites, the Bay was found to be net autotrophic with primary production rates ranging between 0.16 to 3.90 g C m^{-2} day^{-1}. Resource limitation (also known as nutrient addition) assays, undertaken on samples collected at seven sites in the Bay, indicated that phytoplankton productivity was generally limited by nitrogen (N) sources except at Dohles Rocks in the Pine River mouth where silicate was co-limiting with N. Light limited primary production in the lower reaches of the Brisbane River. Phosphate additions had no impact on phytoplankton productivity. Phytoplankton community composition (ratios of the major groups) did not change over the 48 hour incubation period in the resource limitation assays suggesting either the different components of the community had insufficient time to respond or all components responded similarly. Findings from both the resource limitation assays and the bay-wide phytoplankton pigment survey suggest that nitrogen was the major limiting factor of phytoplankton productivity in Moreton Bay in the summer of this study. ❑ *primary productivity, light, nitrate, ammonium, silicate, phosphate, limitation.*

Changes in the characteristic hydrological and physio-chemical nature of estuaries world wide are occurring as a result of increased nutrient inputs (e.g., anthropogenic inputs from waste water treatment facilities and groundwater seepage) associated with urbanization and industrialization, alterations in the magnitude and frequency of freshwater inflows, changes in water circulation patterns (e.g., dredging programs for ship channels) and other human-induced changes including but not limited to tourism. Of these, the most frequently investigated phenomena are eutrophication (Howarth 1988; Howarth & Marino 2006) and harmful algal blooms (Granéli & Turner 2006), which may lead to fish kills (Thronson & Quigg 2008) and the loss of other fauna, flora, and/or habitats (e.g., mangroves; Phillips & Kevekordes 2008). Decreased water quality in Moreton Bay (Fig. 1), an embayment in Southeast Queensland, Australia is no exception. Changing land use patterns, largely driven by rapid coastal development, has increased pressure to develop management strategies to protect marine flora, fauna and habitats whilst providing for human activities. To achieve this, we need to determine how Moreton Bay and other estuaries respond to environmental perturbations. We still lack a clear understanding of specific factors which are important in individual estuarine systems.

Temperature, photosynthetically active radiation (PAR) and nutrients are the main factors controlling algal growth and primary productivity. These factors act synergistically to promote phytoplankton growth but can, in certain combinations, be antagonistic. The role of temperature in primary productivity has been studied under controlled laboratory conditions (Eppley 1972) and *in situ* (e.g. Malone *et al.* 1988; Glibert *et al.* 1995), including in the Logan River and southern Moreton Bay where temperature was found to limit primary productivity during winter but not in summer (O'Donohue & Dennison 1997). Similar findings have been reported for other freshwater and estuarine systems. These seasonal changes in productivity can also be associated with changes in phytoplankton community composition. For example, in Offatts Bayou, a small embayment in south Texas, there is an annual shift in phytoplankton community structure from predominantly diatoms in the winter/spring to predominantly cyanobacteria in the summer (Quigg & Roehrborn 2008). Defining the role of temperature *in situ* is complicated and often modulated by the interactive effects of other factors in controlling productivity, particularly PAR and nutrients.

Experiments based on light-controlled turbidostats (e.g. Quigg & Beardall 2003) and nutrient-controlled chemostats (e.g. Rhee *et al.* 1980) support the general notion that an increase in either PAR or nutrients will result in a corresponding increase in productivity. However these relationships are not as clear in field experiments as productivity measurements show great spatial and temporal variability (e.g. Quigg *et al.* 2007) due to a number of interactive components which cannot be controlled for and, in many cases, are less well defined. In estuaries, the ability of PAR to penetrate the water column is linked to riverine and terrestrial derived freshwater runoff introducing silts, particulates and nutrients. On the oceanic side, water clarity means PAR is often not limiting but nutrient concentrations may be. Hence, along an estuarine (salinity) gradient, phytoplankton productivity responses will be tempered by the availability of PAR and nutrients. This has been shown in Chesapeake and Delaware Bays, USA (Harding *et al.* 1986; Malone *et al.* 1988; Fisher *et al.* 1999), Strait of Georgia, BC (Harrison *et al.* 1991) and Galveston Bay, USA (Quigg *et al.* 2007).

While phytoplankton productivity in some parts of Moreton Bay has been previously reported (e.g., O'Donohue & Dennison 1997), little is known of the year round endemic phytoplankton communities in Moreton Bay (no published studies were available at the time this manuscript was prepared). The report by Dennison & Abal (1999) and studies by Eyre & McKee (2002) and Glibert *et al.* (2006) imply that Moreton Bay phytoplankton communities are potentially under threat from eutrophication. This is supported by the increased frequency of blooms of *Lyngbya majuscula* over the last decade (Bell *et al.* 1999; Ahern 2003; Elmetri & Bell 2004; Albert *et al.* 2005 Ahern *et al.* 2007). Blooms of this benthic cyanobacterium appear to be fuelled by phosphorus-rich waste-water discharge combined with warm, calm conditions

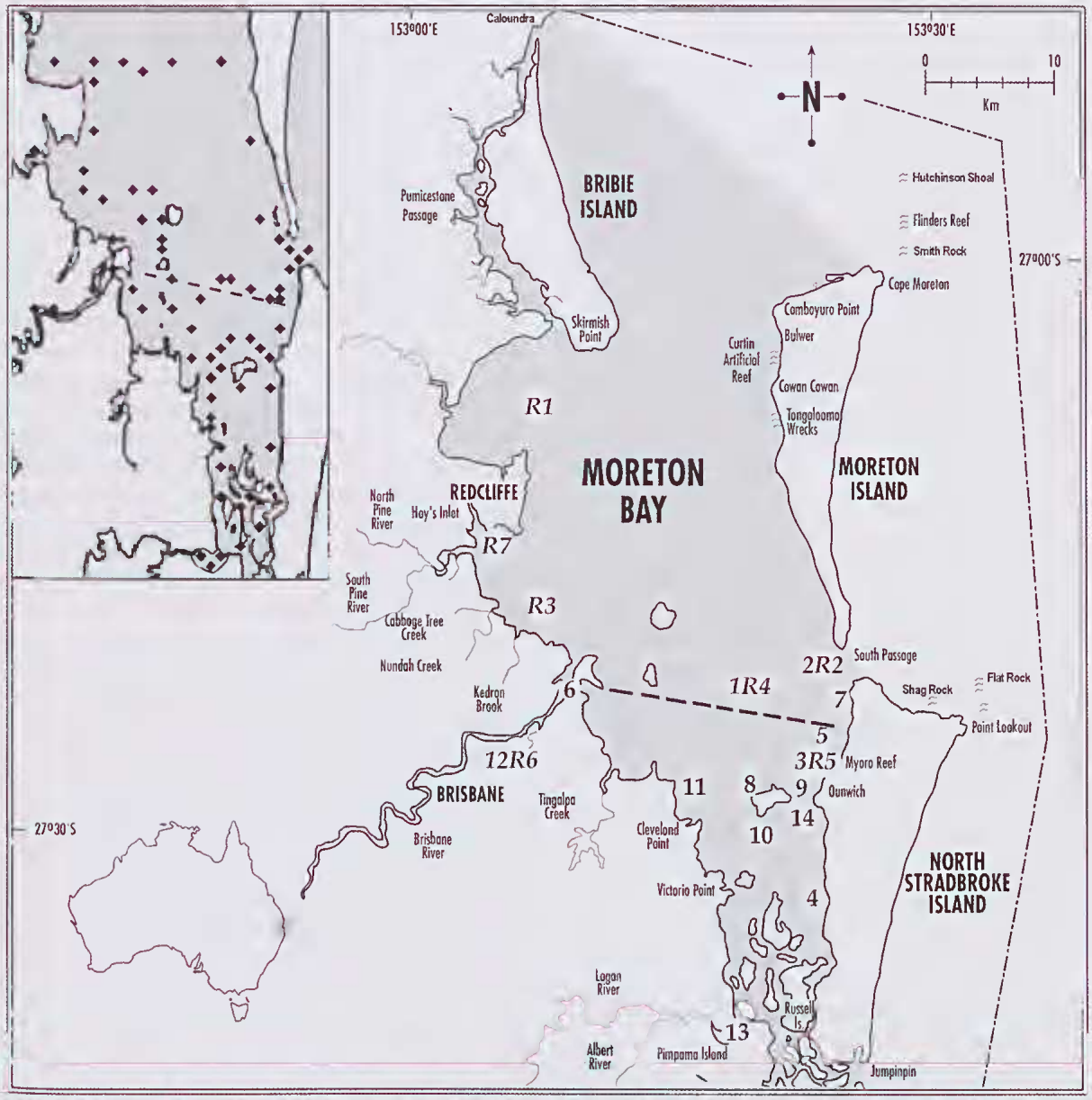

FIG. 1. Moreton Bay (27°S, 153°E) estuary in Southeast Queensland, Australia. Collection sites for resource limitation assays (R1–R7) and primary productivity/respiration studies (1–14), with the corresponding latitudes, longitudes and site description given in Tables 1 & 2. A transect (dashed line) extending from the mouth of the Brisbane River to the Moreton Bay Research Station on North Stradbroke Island was used to present water quality data. Inset map shows the locations of all 73 collection sites. See Table 1 for details.

during summer in an otherwise oligotrophic system. The ability of this species to fix it's own nitrogen allows it to out-compete other phytoplankton. Given the constraints of this workshop, we were not able to conduct a year round study, nor were we able to undertake a careful phytoplankton community analysis. Such efforts are nonetheless warranted. We used pigment analysis to obtain a preliminary insight into the major phytoplankton groups dominating Moreton Bay in the summer.

This current study investigates the role of water quality, PAR and nutrients on the spatial distribution of phytoplankton productivity in

Moreton Bay, Australia during the Thirteenth International Marine Biological Workshop on the Marine Fauna and Flora of Moreton Bay, Queensland (7th to 25th February 2005). Pigment concentrations and ratios were used to examine spatial distributions of phytoplankton groups. Primary productivity and respiration were measured at fourteen sites across the Bay. Resource limitation (nutrient addition) assays were concurrently undertaken for seven sites to determine which resource, if any, limited phytoplankton productivity. The addition of nitrogen (N) as nitrate or ammonium, phosphate, silicate, the combination of all these nutrients (all) and a control (no addition) on phytoplankton growth were examined.

MATERIALS AND METHODS

STUDY SITE

Moreton Bay (27°S, 153°E) is a subtropical estuary in Southeast Queensland, Australia (Fig. 1). Located adjacent to the City of Brisbane (western mainland coast), it is separated from the South Pacific Ocean (east side) by Moreton and North Stradbroke Islands. Moreton Bay covers approximately 1845 km² with an average depth of 6 m (up to 29 m in some areas). Water exchange with the Pacific Ocean occurs via the wide Bay opening to the northeast, South Passage to the east and Jumpinpin in the southern part of the Bay. Terrestrial and freshwater runoff along the western side of the Bay comes from four major river catchments: Brisbane (13,556 km²), Logan/Albert (3650 km²), Pine and Caboolture (together ~ 1820 km²). The largest of these includes the subcatchments of the Upper Brisbane, Stanley, Lockyer, and Bremer Rivers. During dry periods, salt water penetrates into the lower tidal portions of the four major rivers (Steele 1990; Cox 1998). The net movement of water in Moreton Bay, due to tides, creates a pattern of northward water movement on the western side of the Bay and a generally southward water movement on the eastern side. This establishes an overall clockwise pattern of water circulation in the Bay (Newel 1971; Milford & Church 1977; Patterson & Witt 1992).

SAMPLE COLLECTION

Surveys were conducted aboard the *RV Scarus* from 7 to 25 February 2005 at locations indicated on Fig. 1 and detailed in Table 1 (73 sites in total) in order to obtain comprehensive spatial coverage. The sampling regime also included sites situated in the mouth of the four major rivers and in the Bay's three openings to the Pacific Ocean. During survey trips, physical and chemical characteristics of the water were examined at the surface, at 2 m, 4 m and near the bottom (6–9 m) at all sampling sites. The parameters measured with a calibrated Horiba Water Quality Checker Model U-10 (California, USA) included: Salinity (psu), pH (relative units), dissolved oxygen (DO; mg L^{-1}), turbidity (Nephelometric Turbidity Units; NTU) and temperature (°C). Water clarity was determined using Secchi depth (m) measurements. General trends for water quality, found during this study, were well represented by data collected along a transect line (dashed line in Fig. 1) extending 20 km from the Brisbane River to the Moreton Bay Research Station on North Stradbroke Island (designated 0 km and 20 km respectively, in depth profiles, Fig. 2). Discrete water samples were also collected from the surface (0.5 m) in acid-cleaned PVC bottles and transported to the laboratory in the dark (to avoid photo-induced chemical changes) at ambient temperature. These were kept at room temperature (19°C) and at low light (<50 µmol photons m^{-2} s^{-1}) until known volumes were filtered for phytoplankton pigment determination later the same day. At some of these sites, additional water samples were taken for primary productivity measurements (1–14 in Tables 1 & 2) and for resource limitation assays (R1–R7 in Table 1) described below. These experiments were started immediately upon returning to the laboratory.

PRIMARY PRODUCTION

Light-saturated phytoplankton productivity (net, gross productivity and respiration, expressed in g C m^{-2} day^{-1}) was determined using the light-dark bottle method of Strickland & Parsons (1972). Each seawater sample, collected from discrete sites (1–14 in Fig. 1, Tables 1 & 2), was decanted into 7 acid-washed glass Biological Oxygen Demand (B.O.D.) bottles (250 mL). Each bottle was filled to overflowing to avoid air bubbles. Three bottles were used for the light treatments and two bottles, wrapped in

foil, were used for the dark treatments. Two additional bottles, with buffered Formalin (10% final), were used as controls to assess the impact of abiotic reactions on dissolved O_2 levels in light and dark conditions. The initial DO concentration (mg O_2 L^{-1}) was measured in the original source water from each collection site. Treatment bottles were incubated in an outdoor water bath at ambient temperature (± 3°C), maintained with a circulating water pump, under 50% of ambient sunlight. Bottles floated near the surface of the incubator but did not overlap. Phytoplankton responses to each treatment were determined by measuring the change in DO concentration using a YSI Environmental Oxygen Probe (John Morris Scientific Pty Ltd). Daily net/gross productivity and respiration were calculated by taking into account the 13:11 light:dark period at this time of year. Oxygen produced was converted to carbon fixed, using a photosynthetic quotient of 1.2 and a respiratory quotient of 1.0 (Laws 1991). Values were expressed, per square metre, as we totalled rates to the base of the euphotic zone by multiplying productivity by Secchi depth (Wetzel & Likens 2000).

The ratio of the dark respiration rate to the photosynthetic (gross) rate (RR:GPR ratio) has been proposed as a useful parameter in evaluating primary productivity measurements on natural phytoplankton communities (Verity 1982); that is, whether a phytoplankton community is net autotrophic. In addition, we also assessed net growth efficiency which Falkowski *et al.* (1985) defined as the ratio of net to gross photosynthesis. This ratio quantifies the amount of photosynthetically fixed carbon that is lost in relation to that used for new growth.

RESOURCE LIMITATION BIOASSAYS

Two-day resource limitation bioassays were undertaken to identify which resource (nutrient (s) and/or light) limited phytoplankton growth at sampling sites in Moreton Bay during the period of investigation. These bioassays were carried out essentially as described by Fisher *et al.* (1999) on water samples collected from seven sites (R1 to R7 in Fig. 1, Table 1). Surface (top 0.5 m) water (8 L) was collected, stored in a cool, low light area of the boat, until we returned to the laboratory (< 4–6 hrs). Immediately before starting the bioassays, a subsample was taken for pigment analysis. Aliquots (1 L) of water sample were subsequently placed into acid washed containers and each received one of the following nutrient additions (final concentrations in each treatment): +N-nitrate (30 µmol L^{-1} NO_3), +N-ammonium (30 µmol L^{-1} NH_4^+), +P (2 µmol L^{-1} PO_4^{3-}), +Si (30 µmol L^{-1} SiO_3), All (30 µmol L^{-1} NO_3^-, 30 µmol L^{-1} NH_4^+, 2 µmol L^{-1} PO_4^{3-} and 30 µmol L^{-1} SiO_3) and a control (no addition). Treatments were incubated at ambient temperature under 50% ambient sunlight in an outdoor facility described above. Subsamples (≥4) were harvested for pigment analysis, from control and nutrient treatments, at identical times over the 48 hr incubation period to assess changes in phytoplankton biomass. The response potential of phytoplankton in each treatment was quantified using the phytoplankton response index (PRI) which calculates the phytoplankton growth response using the maximum biomass relative to the initial biomass and the time taken to reach the maximum biomass (Fisher *et al.* 1999). We also included a response classification (as recommended by Fisher *et al.* 1999) to accommodate for errors and temperature differences between assays; the threshold for a significant response was set to 140% > than the control.

Given the time and resource constraints of the workshop and the questions we were seeking to address, water samples were collected from seven sites across the Bay for resource limitation bioassays at the expense of experimental replication, that is, we did not have replicate bottles for each treatment. As our findings are consistent within bioassays and across assays on samples, collected from sites with similar water quality, our findings are nonetheless significant.

PIGMENT ANALYSIS

A known volume of water was filtered through a Whatman GF/F filter under low pressure (< 130 kPa) and immediately frozen. Filters were thawed on ice and pigments extracted in 100% acetone overnight at 4°C in darkness. Immediately prior to spectrophotometric analysis, the acetone was diluted to 90% with distilled water and the sample stirred with a vortex mixer. The filter was removed from the sample and the supernatant centrifuged for 10

mins at 5000g to remove any remaining particulates. High performance liquid chromatography (Jeffrey *et al.* 1997) is the current method used for assessing phytoplankton composition based on pigment profiles. However, given this was not available, we used earlier spectrophotometric methods. Concentrations of the pigments, listed below, were calculated as follows: Chlorophyll (chl) *a* using the equations in SCOR-UNESCO (1966); cyanobacterial (cyano) pigment using the equation by MacKinney (1941); carotenoids in Chlorophyta/Cyanobacteria (Chloro/Cyano) and Chrysophyta/Pyrrophyta (Chryso/Pyrro) using the equations of Strickland & Parsons (1972). Phycocyanin and phycoerythrin were estimated according to information at http//pubs.water.usgs.gov/twri9A from the ratio of wavelengths 652:665 and 615:665 respectively (no units).

Means ± standard deviations are presented for field measurements and lab-based results.

RESULTS

PHYSICAL AND CHEMICAL WATER ANALYSES

Generally, vertical water profiles for salinity, turbidity and DO at 73 sites across Moreton Bay indicated a well mixed water column given that there were no significant differences in values at the surface relative to bottom waters (Table 1). Along a transect line (shown in Fig. 1) from the Brisbane River mouth (0 km) to Moreton Bay Research Station (20 km), vertical profiles (Fig. 2) for salinity, turbidity and DO showed a clear gradient for each parameter extending across the Bay. Salinity readings ranged from 34 ±2 psu, recorded in surface waters in the mouth and lower Brisbane River, increasing to 38 ±0.5 psu near North Stradbroke Island (Fig. 2A). The salinity gradient recorded along this transect is typical for the Bay with lower salinity levels, due to riverine runoff, on the landward side increasing towards the oceanic side of the Bay (see also Table 1). At the time of the study, 82% of measured salinities were ≥ 34 psu (n = 196 of 239 measurements; Table 1) indicating that the oceanic influence dominated Moreton Bay salinities. High salinity levels were also recorded in the mouths of the Logan River (37±0.3 psu) and Pine/Caboolture Rivers (35±0.5 psu).

Highest turbidity (NTU) levels were measured near the four major river outlets and along coastlines flanking dense residential areas of Brisbane (Table 1). Depth profiles along the 20 km transect line showed high turbidity levels (36–44 NTU) on the landward side of the Bay, decreasing by 50% some 8 km from the Brisbane River mouth and then to 0–4 NTU near North Stradbroke Island (Fig. 2B). In Moreton Bay, a curvilinear relationship was found between turbidity and Secchi depth (Fig. 3A) with the highest turbidity readings recorded in areas with the lowest water clarity (Table 1). Secchi depths were as shallow as 0.7 m, 2–3 km up the mouth of the Brisbane River (corresponding turbidity of 15 NTU) and as deep as 7.5 m at sites in the northern and eastern parts of the Bay (< 5 NTU). In general, Secchi readings along the landward coastline and river openings were < 1 m (Table 1).

Lowest DO concentrations were recorded in areas of highest turbidity (r^2 = 0.79) near the mainland coastline, with DO values increasing towards the oceanic end of the transect (Fig. 2C). Water temperature and pH did not vary significantly in Moreton Bay during the course of this study (not shown). Surface water temperatures averaged 27.7°C (±1.2°C, n = 111) and there was a 1–2°C temperature range in the water column to a depth of 9 m. The average pH was 7.88 (±0.10, n = 75) across Moreton Bay, except for several sample sites in the Brisbane River where surface water pH ranged from 7.2–7.5.

PIGMENT DISTRIBUTIONS

Chl *a*, measured as a proxy for phytoplankton biomass in surface waters, averaged 2.80 (±1.75) µg L^{-1} across the 73 sites in the Bay (Table 1). Phytoplankton pigment concentrations were generally highest in areas with lower water clarity (Secchi depths < 3.25 m, Fig. 3B, Turbidity < 25 NTU, Fig. 3C); this was particularly evident in the mouths of the four major rivers (Table 1). The highest concentrations of Chl *a* (5.26–6.93 µg L^{-1}) were recorded in waters with Secchi depths <1.7 m (Fig. 3B). There was no significant relationship between Chl *a* concentrations and turbidity (Fig. 3C) indicating PAR did not substantially control phytoplankton biomass distribution.

Generally, the bay-wide survey of pigments showed no clear distribution pattern of phytoplankton groups in Moreton Bay. Ratios of

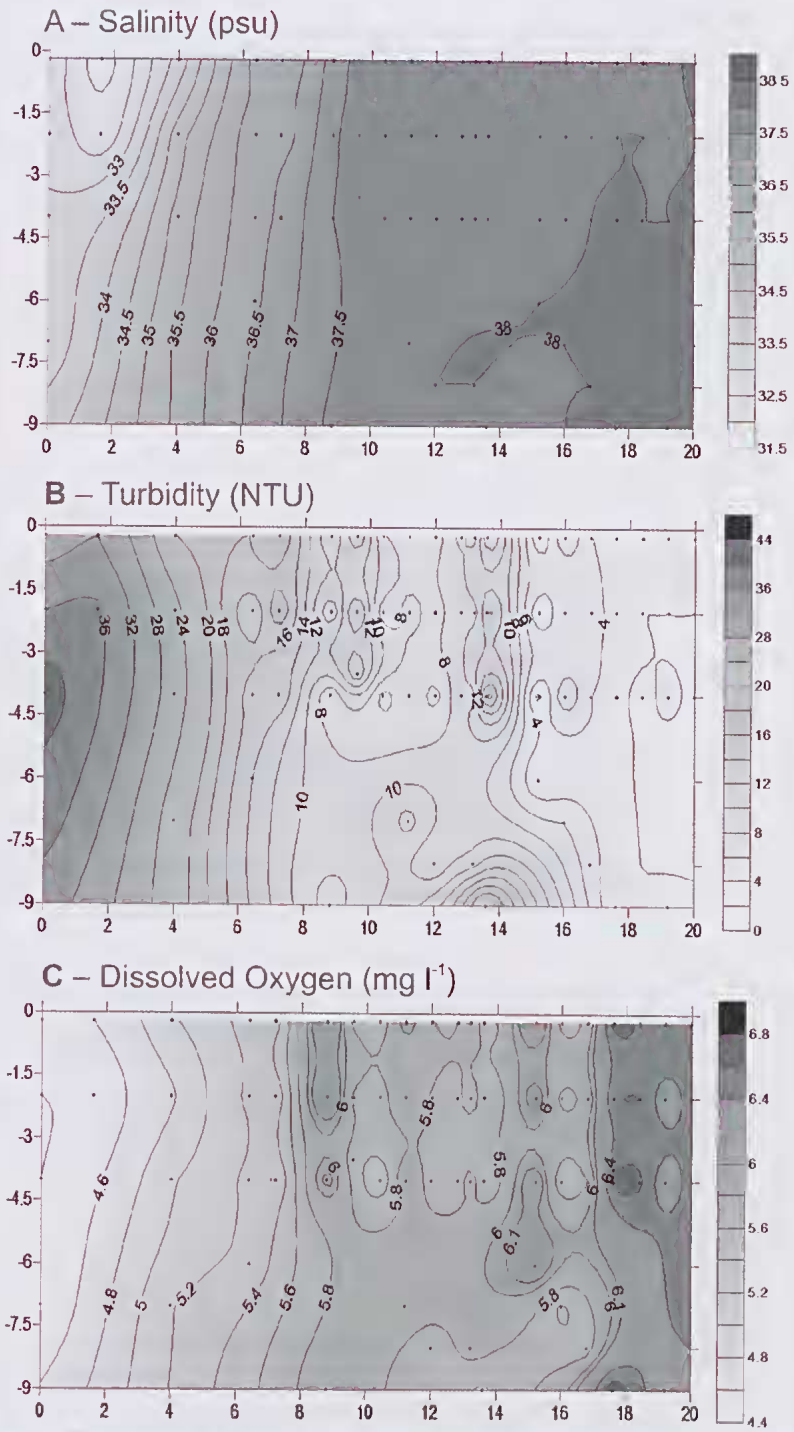

FIG. 2. Water quality parameters were measured across the entire Moreton Bay estuary. Data collected along a 20 km transect (shown in Fig. 1) represents the general landside-to-seaside trends for this Bay. Distance, shown on the x-axis, extends from the mouth of the Brisbane River (0 km) to the Moreton Bay Research Station (20 km). Dots on the contour maps indicate sampling sites in the water column with depth (m below the surface) plotted on the y-axis. Profile values are presented in the legend to the right for each water quality parameter. (A) Salinity (psu), (B) turbidity (NTU) and (C) dissolved oxygen (mg l^{-1}).

Table 1. Water quality and pigment data for 73 sampling sites throughout Moreton Bay. Given the homogenous nature of the vertical water column, averages (± standard deviations) are given for salinity (psu), turbidity (NTU) and dissolved oxygen (DO; mg l^{-1}). Secchi (m) depth was measured at each site. Pigment concentrations were measured in surface samples only. Chlorophyll a (Chl a; µg L^{-1}), Cyanobacteria (Cyano; µg L^{-1}), carotenoids in Chlorophyta/Cyanobacteria (Chloro/Cyano) and Chrysophyta/Pyrrophyta (Chryso/Pyrro), phycocyanin:chlorophyll a and phycoerythrin:chlorophyll a (estimated as ratio of wavelengths 652:665 and 615:665 respectively; no units) were used to examine the phytoplankton community composition. Water sample collection sites for primary productivity (gross and net) and respiration rate measurements (1–14) and resource limitation assays (R1–R7) (see also Fig.1).

Expt	Site Location	Latitude South	Longitude East	Salinity (psu)	Turbidity (NTU)	DO (mg L^{-1})	Secchi (m)	Chl a (µg L^{-1})	Cyano (µg L^{-1})	Chloro/ Cyano	Chryso/ Pyrro	Phyco-cyanin/ Chl a	Phyco-erythrin/ Chl a
14	Adam's Beach	27.5083	153.2357	38.08(0.05)	4.75(0.96)	6.42(0.15)	2.5	3.80	4.56	1.37	3.43	0.44	0.23
	Between Peel I. & Dialba Passage	27.4760	153.3707	38.00(0.08)	4.25(0.50)	4.69(2.25)	2	3.67	4.25	1.23	3.07	0.44	0.24
	Between Lazaret Gutter & Maroom Bank	27.4678	153.3547	38.00	4.75(0.50)	6.03(0.07)	2	2.68	3.09	1.12	2.80	0.57	0.36
	NW of Peel I.	27.4720	153.3368	37.95(0.06)	4.25(0.96)	5.99(0.03)	2.5	2.47	2.82	0.83	2.07	0.54	0.33
	WNW of Peel I.	27.4888	153.3180	37.95(0.06)	4.50(1.29)	6.26(0.10)	3	2.83	3.27	1.05	2.63	0.54	0.35
	W of Peel I.	27.5085	153.3203	37.95(0.06)	6.00(1.41)	6.10(0.11)	2.2	2.37	2.73	0.80	2.00	0.49	0.27
	N of Toondah Harbour entrance	27.5347	153.3042	37.87(0.06)	11.00(1.73)	5.64(0.09)	1.6	2.63	3.04	0.96	2.40	0.47	0.27
	N of Point Halloran	27.5562	153.3073	38.03(0.06)	10.67(4.62)	5.81(0.14)	1.8	2.60	3.00	0.93	2.33	0.46	0.21
	Point Halloran	27.5678	153.3083	38.00	7.33(0.58)	5.84(0.06)	2	2.61	3.00	0.99	2.47	0.48	0.31
	E of Victoria Point	27.5855	153.3188	37.90(0.14)	7.25(0.96)	5.90(0.12)	2	2.67	3.09	1.00	2.50	0.49	0.29
	NE of Redland Bay	27.6065	153.3180	38.03(0.05)	7.50(1.73)	5.66(0.04)	2	2.39	2.73	0.88	2.20	0.49	0.28
	SE of Redland Bay	27.6228	153.3227	37.93(0.10)	10.75(1.26)	5.62(0.05)	1.8	1.76	2.01	1.04	2.60	0.56	0.37
	Between Point Talburpin & Karragarra I.	27.6405	153.3412	37.97(0.06)	10.67(3.79)	5.47(0.10)	1.6	1.56	1.79	0.71	1.77	0.46	0.28
13	Logan River mouth	27.7043	153.3203	37.20(0.28)	36.00(19.80)	5.08(0.20)	1.2	5.26	6.17	1.99	4.97	0.48	0.26
	Between Logan River mouth & Russell I.	27.6893	153.3420	37.80	52.50(0.71)	5.31(0.07)	0.7	6.43	7.60	2.48	6.20	0.46	0.26
	W of Russell I.	27.6697	153.3563	38.10(0.10)	14.00(0.75)	5.35(0.05)	1.7	1.42	1.43	0.53	1.33	0.82	0.40
	W end, Macley/Karragarra Is Channel	27.6337	153.3568	38.10	26.25(3.30)	5.61(0.12)	1	2.97	3.13	1.28	3.20	0.61	0.39
	E of Lamb I.	27.6238	153.3928	38.08(0.05)	21.00(2.71)	5.55(0.16)	1	4.05	4.56	1.55	3.87	0.51	0.26
4	Near Blakesley's Anchorage	27.5843	153.4028	37.87(0.06)	11.67(1.53)	5.46(0.07)	1.5	4.08	4.65	1.57	3.93	0.55	0.37
	One Mile Anchorage	27.4872	153.4010	38.00(0.14)	4.50(0.71)	7.16(0.13)	2.5	2.11	2.42	0.72	1.80	0.34	1.00
9	S of Dunwich, in Deanbilla Bay	27.5083	153.4023	37.87(0.06)	6.67(0.58)	6.39(0.17)	1.75	3.39	3.98	1.36	3.40	0.56	1.10
3/R5	NE end of Dialba Passage	27.4757	153.3918	37.88(0.88)	2.40(1.14)	6.61(0.11)	3.2	2.06	2.37	0.76	1.90	0.51	1.05
	Amity Channel, near Fingue Passage	27.4352	153.4070	37.93(0.05)	2.75(0.50)	6.77(0.04)	4.5	0.85	0.89	0.25	0.63	0.44	0.98
2/R2	South Passage Bar, near Amity	27.3863	153.4512	37.80(0.14)	9.50(4.95)	7.09(0.12)	2.5	1.15	1.16	0.31	0.77	0.32	0.94
	Rainbow Channel, between Amity/Kooringal	27.3765	153.4337	37.77(0.05)	3.67(1.70)	6.89(0.16)	3.25	1.21	1.39	0.72	1.80	0.65	1.35
7	NW Amity, E entrance to Rous Channel	27.3877	153.4338	37.80	2.00(1.00)	7.14(0.04)	5	1.64	1.88	0.81	2.03	0.61	1.23
	Rainbow Channel, Amity Point	27.4000	153.4338	37.78(0.08)	2.00(0.71)	6.97(0.07)	3	1.75	2.01	0.65	1.63	0.66	1.05
5	NE corner Amity Banks	27.4183	153.4087	37.90	4.50(1.50)	7.10(0.04)	2	1.36	1.52	0.65	1.63	0.73	1.20
	Rainbow Channel / Cooloolo Passage	27.4405	153.4083	37.98(0.08)	6.25(3.70)	7.03(0.02)	2.5	1.11	1.25	0.56	1.40	0.68	1.17
	Amity Banks, near Cooloolo Passage	27.4403	153.4040	37.90	5.00(1.00)	6.89(0.05)	2.2	3.04	3.58	1.35	3.37	0.60	1.16
	Between Lazaret Gutter / Maroom Banks	27.4677	153.3548	37.95(0.05)	4.50(0.50)	5.83(0.04)	2.5	2.28	2.51	0.61	1.53	0.54	0.40
	NW Peel I.	27.4722	153.3370	37.93(0.04)	7.00(1.00)	5.70(0.04)	2.5	3.29	3.91	1.27	3.17	0.50	0.29
11	N of Cleveland Point	27.5000	153.2925	37.83(0.08)	19.00(3.39)	5.57(0.05)	1.2	2.81	3.27	0.99	2.47	0.45	0.99
	N of Raby Bay	27.5043	153.2728	37.77(0.05)	10.33(0.47)	5.70(0.06)	1.75	4.54	5.28	1.69	4.22	0.47	0.25
	ENE of Wellington Point	27.4737	153.2732	37.90(0.07)	8.75(1.30)	6.02(0.04)	2	2.33	2.68	0.80	2.00	0.54	0.33
	N of Wellington Point	27.4512	153.2550	37.95(0.05)	6.75(1.09)	5.75(0.05)	2			1.20	3.00	0.54	0.36
	Waterloo Bay, N area	27.4515	153.2193	37.76(0.05)	6.33(1.25)	5.60(0.14)	1.5	2.80	3.27	1.03	2.57	0.54	0.33
8	Between Wynnum & Green I.	27.4335	153.2033	37.76(0.05)	16.33(0.47)	5.71(0.02)	1.2	4.46	5.28	1.71	4.27	0.47	0.24
	Between Lytton & Fishermans I.	27.4003	153.1573	36.26(0.25)	18.66(1.89)	5.24(0.05)	1.1	6.16	7.34	2.63	6.57	0.48	0.23

Table 1 (continued) ...

Expt	Site Location	Latitude South	Longitude East	Salinity (psu)	Turbidity (NTU)	DO (mg L^{-1})	Secchi (m)	Chl a (µg L^{-1})	Cyano (µg L^{-1})	Chloro / Cyano	Chryso / Pyrro	Phyco-cyanin / Chl a	Phyco-erythrin / Chl a
12/R6	Brisbane River, near Breakfast Creek	27.4408	153.0413	33.02(0.08)	36.25(4.71)	4.47(0.09)	1.2	6.66	7.96	2.64	6.60	0.50	0.25
	Breakfast Creek, joining Brisbane River	27.4383	153.0413	31.85(0.15)	34.50(2.50)	4.52(0.08)	1	2.76	3.22	1.07	2.67	0.53	0.32
6	Brisbane River, near Gateway Bridge	27.4408	153.0883	34.82(0.71)	23.25(2.38)	4.91(0.10)	1	4.08	4.89	1.63	4.07	0.51	0.28
	Brisbane R. between Pinkenba/Bulwer I.	27.4195	153.1378	36.30(0.07)	15.25(1.64)	5.26(0.02)	1.5	5.49	6.53	2.20	5.50	0.47	0.23
	Luggage Point, Brisbane River mouth	27.3738	153.1563	36.35(0.05)	16.50(1.50)	5.80(0.08)	1.4	3.08	3.62	1.25	3.13	0.47	0.23
	N of Fisherman's I.	27.3418	153.1833	37.42(0.15)	7.75(1.48)	6.35(0.11)	1.7	6.91	8.32	2.73	6.83	0.49	0.24
	Between Fisherman's Is & Mud I.	27.3588	153.2177	37.60(0.08)	29.67(0.47)	5.91(0.07)	1	6.21	7.43	2.43	6.07	0.50	0.29
	Between St Helena Is & Mud I.	27.3680	153.2408	37.80(0.07)	9.50(2.06)	6.04(0.14)	1.5	5.68	6.80	2.14	5.36	0.50	0.29
	Fisherman's Gutter, Boolong Bank	27.4015	153.3257	38.00	1.75(0.43)	6.27(0.05)	2	1.56	1.82	0.60	1.51	0.44	0.21
1/R4	Rous Channel, near Amity Point	27.4048	153.3717	38.05(0.05)	2.75(0.43)	6.65(0.05)	2.5	1.93	2.28	0.83	2.08	0.54	0.36
	Moreton Banks, near Rous Channel	27.3702	153.3905	38.00	2.00(0.82)	6.60(0.04)	3.2	1.04	1.21	0.54	1.34	0.50	0.28
	Rous Channel / Rainbow Channel banks	27.3762	153.4265	38.07(0.04)	1.50(0.5)	6.54(0.05)	3.2	0.95	1.07	0.40	1.00	0.53	0.32
10	South West Rocks, Peel I.	27.5203	153.3557	37.75(0.11)	5.00(1.87)	6.18(0.02)	7.5	0.11	0.09	0.21	0.52	0.68	0.70
	Rainbow Channel, near Myora	27.4672	153.4068	37.97(0.08)	3.00(0.71)	6.30(0.07)	2.2	2.18	2.57	0.85	2.13	0.49	0.30
	Between Lazaret Gutter / Maroom Banks	27.4672	153.3545	38.07(0.08)	3.00	5.70(0.07)	3	1.43	1.68	0.60	1.50	0.46	0.27
	W entrance to Rous Channel	27.4255	153.3027	38.17(0.04)	1.00	6.35(0.08)	4	0.96	1.07	0.47	1.17	0.44	0.26
	N point of St Helena I.	27.3767	153.2412	38.10	6.50(1.12)	6.14(0.25)	1.5	0.92	1.05	0.50	1.25	0.57	0.34
	Between Fishermans Is & Mud I.	27.3587	153.2267	38.20	9.00(0.82)	6.08(0.08)	1.2	0.87	0.94	0.43	1.07	0.68	0.46
	N of Fisherman's I.	27.3392	153.1933	37.80(0.16)	10.25(1.09)	5.89(0.04)	2	2.87	3.40	1.19	2.98	0.46	0.24
R3	E of Nudgee	27.3372	153.1420	37.35(0.35)	13.00(3.00)	6.28	1.5	6.08	7.25	2.41	6.02	0.47	0.24
	E of Shorncliffe / Cabbage Tree Creek	27.3222	153.1087	37.43(0.26)	13.67(1.70)	6.29(0.14)	1.4	2.17	2.53	1.11	2.78	0.51	0.27
	Cabbage Tree Creek	27.3343	153.0743	33.95(1.65)	21.50(4.50)	4.50(0.22)	1.1	5.52	6.58	2.33	5.83	0.55	0.29
	Bramble Bay, NE of Shorncliffe	27.3028	153.1003	37.30(0.08)	19.33(3.30)	5.72(0.04)	1.5	1.57	1.83	0.88	2.20	0.54	0.33
R7	Pine River, closest to Dohles Rocks	27.2752	153.0420	35.35(0.25)	17.50(2.50)	5.79(0.16)	1.25	6.93	8.32	3.74	9.36	0.50	0.27
	E of Scott's Point, Redcliffe	27.2515	153.1208	37.36(0.12)	14.00(4.24)	5.63(0.18)	1.5	2.23	2.62	1.29	3.22	0.53	0.29
	E of Scarborough	27.2038	153.1252	37.43(0.15)	8.25(1.09)	5.55(0.27)	2.2	1.64	1.91	0.80	2.00	0.53	0.31
	Deception Bay, NW of Scarborough	27.1758	153.0733	37.50	20.00	6.21(0.16)	1.1	4.52	5.28	2.43	6.07	0.56	0.37
R1	NE of Scarborough	27.1752	153.1545	37.50(0.25)	6.75(2.59)	6.08(0.04)	2.2	1.57	1.83	0.83	2.07	0.56	0.41
	ENE of Scarborough	27.1760	153.1850	37.68(0.15)	6.50(1.12)	6.07(0.04)	1.9	1.65	1.83	0.72	1.80	0.54	0.36
	Pearl Channel	27.1837	153.2178	37.70(0.07)	3.00(0.71)	6.04(0.05)	3	1.12	1.27	0.69	1.72	0.63	0.63
	E of Pearl Channel	27.1743	153.2590	37.83(0.15)	3.00(1.00)	6.02(0.02)	3.7	0.61	0.67	0.37	0.92	0.55	0.33
	WNW of Tangalooma, Moreton I.	27.1595	153.3203	37.78(0.08)	1.75(0.83)	6.10(0.04)	6.7	0.32	0.34	0.23	0.58	0.75	0.43
	Moreton Banks, near Rous Channel	27.2925	153.3563	37.68(0.40)	5.25(2.49)	5.79(0.03)	6	0.62	0.69	0.21	0.52	0.60	0.43
	Fisherman's Gutter	27.4020	153.3373	37.87(0.05)	4.33(2.49)	5.75(0.18)	3.5			0.10	0.24	0.59	0.41

Table 2. Primary productivity (gross and net photosynthesis) and respiration rates (water sample collection sites shown on Fig. 1). Ratio of dark respiration to gross photosynthesis (RR:GPR ratio) and ratio of net to gross photosynthesis (also referred to as net growth efficiency) are used to evaluate primary productivity measurements on natural phytoplankton communities.

Site no.	Site Location	Gross photo-synthesis rate (g C m^{-2} day^{-1})	Net photo-synthesis rate (g C m^{-2} day^{-1})	Respiration rate (g C m^{-2} day^{-1})	RR:GPR ratio	Net growth efficiency (NPR:GPR)
1	Rous Channel, middle	-0.006	-0.084	0.077		
2	South Passage Bar, near Amity	-0.080	-0.122	0.042		
3	Northeast end of Dialba Passage	0.224	0.158	0.065	3.44	0.71
4	Near Blakesley's Anchorage, South of Dunwich	0.690	0.571	0.119	5.79	0.83
5	Amity Banks, Northeast corner	0.648	0.603	0.045	14.41	0.93
6	Brisbane River, near Gateway Bridge	0.893	0.859	0.034	26.46	0.96
7	Northwest Amity, East entrance to Rous Channel	1.481	0.975	0.506	2.93	0.66
8	Between Wynnum & Green Island	1.257	1.155	0.101	12.41	0.92
9	South of Dunwich in Deanbilla Bay	1.277	1.248	0.030	43.25	0.98
10	South West Rocks, Peel Island	1.906	1.420	0.486	3.92	0.74
11	North of Cleveland Pt	1.531	1.477	0.054	28.35	0.96
12	Brisbane River, near Breakfast Creek	3.231	2.252	0.979	3.30	0.70
13	Logan River mouth	3.113	2.390	0.724	4.30	0.77
14	Adam's Beach, North Stradbroke I.	4.062	3.900	0.162	25.07	0.96

Chlorophyta/Cyanobacteria (0.10–3.74) and Chrysophyta/Pyrrophyta (0.24–9.36) (Table 1) however, revealed that when water clarity was low (1.2±0.27 m) and turbidity was relatively high (22±13 NTU), Chlorophyta predominated over Cyanobacteria (Chloro/Cyano > 2). When Cyanobacteria predominated over Chlorophyta (Chloro/Cyano ≤ 0.37), water clarity was high (4.9 ±1.7 m) and turbidity was very low (4.5±2.3 NTU). There was no correlation with water

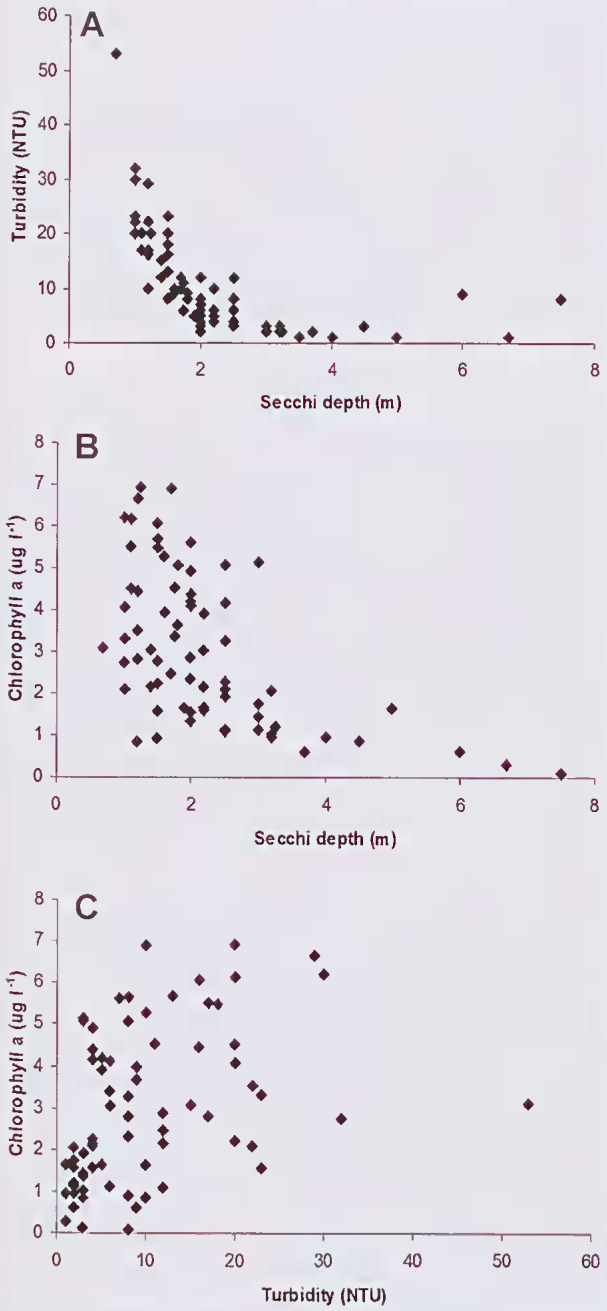

FIG. 3. Primary productivity is controlled to a large extent by the ability of PAR to penetrate the water column. A. Based on samples, collected across Moreton Bay, there is a curvilinear relationship between turbidity (NTU) and water clarity (Secchi depth, m). B. There was no empirical relationship between chlorophyll a ($\mu g\ l^{-1}$), often used as a proxy for phytoplankton biomass, and water clarity (Secchi depth, m). C. There is no relationship between chlorophyll a ($\mu g\ l^{-1}$) and turbidity (NTU).

quality or location in Moreton Bay when Chloro/Cyano ratios ranged between 0.37–1.99 (Table 1). Similarly, ratios of Chrysophyta/Pyrrophyta show Chrysophyta (Chryso/Pyrro > 5) favoured regions of Moreton Bay with high turbidity (≥22 NTU) while Pyrrophyta (Chryso/Pyrro < 1) were more prominent in areas of low turbidity (≤5 NTU) (Table 1). Again, there was no correlation in the distribution of Chrysophyta/Pyrrophyta with water quality or location in Moreton Bay when Chryso/Pyrro ratios ranged between 1–5 (Table 1).

Phycocyanin and phycoerythrin are found predominately in Cyanobacteria and Cryptophyta (Jeffrey *et al.* 1997) however plastids of the genus *Dinophysis* in the Pyrrophyta also contain phycoerythrin. Phycocyanin and phycoerythrin were present, on average, in relative concentrations of 0.53 (±0.08) and 0.45 (±0.30) respectively (Table 1). There was no clear association of phycocyanin distributions with either water quality parameters or other pigments (Table 1). In general (52 of the 73 sites), relative concentrations of phycoerythrin were <0.40 (Table 1) indicating low levels in the Bay. However, elevated phycoerythrin levels (1.11 ±0.12, n = 11) were recorded along the northern reaches of North Stradbroke I. near Amity Point extending into South Passage. This stretch of water had low turbidity (4.5±2.2 NTU) and high water clarity (2.95 ±0.97 m).

PRIMARY PRODUCTIVITY

Twelve of the fourteen sites, sampled throughout Moreton Bay were net autotrophic with daily net production rates varying from 0.16 to 3.90 g C m^{-2} day^{-1} (Table 2, Fig. 1). Primary productivity (net photosynthesis) measurements showed variability on the eastern side of Moreton Bay. The highest primary productivity rate (3.9 g C m^{-2} day^{-1}) in the Bay was measured in the Adam's Beach sample (Site 14), North Stradbroke Island. The lowest three net primary productivity rates (Sites 3, 4, 5) were measured from samples also collected from the eastern section of the Bay, offshore of North Stradbroke Island. Primary productivity rates from the Deanbilla Bay sample, North Stradbroke Island (Site 9) were 2 to 8-fold higher than those from samples at Sites 3, 4 and 5 but, 3–fold less than rates from the sample collected nearby at Adam's

Beach (Site 14). Samples from Sites 1 & 2, near the South Passage, were net heterotrophic (Fig. 1, Table 2) while the sample collected near South Passage at the east entrance of Rous Channel (Site 7) had a primary productivity rate of 0.975 g C m^{-2} day^{-1}.

In the western bay, samples collected from sites located near the mouth or just north of the Brisbane River (Sites 6, 8) tended to have relatively low primary productivity rates (0.86–1.15 g C m^{-2} day^{-1}) whereas samples in the central bay, south of the Brisbane River (Sites 10, 11), had slightly higher daily net production rates of 1.42 to 1.48 g C m^{-2} day^{-1}. Higher rates were recorded in samples collected in the Brisbane River near Breakfast Creek (Site 12, 2.25 g m^{-2} day^{-1}) and at the Logan River mouth (Site 13, 2.39 g C m^{-2} day^{-1}).

Respiration rates varied more than 30-fold across the Bay, with rates ranging between 0.03 to 0.98 g C m^{-2} day^{-1} (Table 2). The RR:GPR ratios at sampling sites, along the mainland coast, ranged from 12.41 to 28.35 (Sites 6, 8 & 11) while ratios of 3.3 and 4.3 were measured in samples collected in the Brisbane River, near Breakfast Creek (Site 12), and the Logan River mouth (Site 13) respectively. Excluding the two net heterotrophic sites near South Passage (Sites 1 & 2), net growth efficiencies ranged from 0.66–0.98 in samples collected across Moreton Bay (Table 2, Fig. 1).

RESOURCE LIMITATION BIOASSAYS

Bioassays revealed that in 6 of the 7 sites N, as nitrate, ammonium or both, was the limiting resource (R1–R5 Fig. 4A–E, R7, Fig. 4G). The PRI was well above the threshold (140%, see methods) in treatments where N was added. Phytoplankton responded well when all nutrients were added, yielding PRI values of around 800 or greater (Fig. 4) in samples collected from all seven sites in Moreton Bay (R1–R7 in Figs. 1, 4A–4G). Light was found to be the limiting factor in the water sample taken in the Brisbane River near Breakfast Creek (R6 in Fig.1; Fig. 4F), as phytoplankton growth was similar in the control and the nutrient treatments. At Dohles Rocks, near the Pine River mouth, phytoplankton growth was co-limited by N-sources and silicate (R7 in Fig. 1; Fig. 4G). Phosphate and silicate were generally not limiting to phytoplankton production during the period of this study in Moreton Bay (Fig. 4).

Ratios of Chloro/Cyano and Chryso/Pyrro which accounted for 37 to 52% and 48 to 63% of the communities respectively, remained relatively constant over the 48 hr incubation period (see example; Fig. 4H) irrespective of treatments or sample locations. This is indicative of the lack of a specific response by these phytoplankton groups to the addition of nutrients.

DISCUSSION

Present and previous investigations on primary productivity (e.g. O'Donohue & Dennison 1997; Eyre & McKee 2002; Glibert *et al.* 2006) have clearly established Moreton Bay as a complex, dynamic system in which differing spatial and temporal patterns are observed. Temperature limits primary productivity during winter (O'Donohue & Dennison, 1997) while nutrients are more important during summer (O'Donohue & Dennison 1997; Eyre & McKee 2002; Glibert *et al.* 2006; present study). Additional factors affecting primary productivity in Moreton Bay include salinity, turbidity, DO gradients (Fig. 2), PAR (Fig. 3) as well as bay hydrodynamics (Newel 1971; Milford & Church 1977; Patterson & Witt 1992). In the northern section of the Bay, the Pacific Ocean plays an important role in flushing the system. A clockwise current operating in the upper portion of the Bay carries riverine outflow north along the western coastline. To the south, water quality is patchy due to the large number of islands and a comparatively smaller oceanic opening via Jumpinpin. Overlying these factors is the occurrence of big events such as cyclones and continuing anthropogenic disturbances such as effluent discharge, mangrove clearing, shipping and recreational activities that occur in the Bay and surrounding catchments.

Phytoplankton productivity in Moreton Bay measured in the present study (0.16 to 3.90 g C m^{-2} day^{-1}; Table 2) was higher than that previously reported in this estuary by O'Donohue & Dennison (1997). The disparity in results may be due to different methods (light/dark bottle method in current study versus C14 method in the earlier study) or to different sampling regimes (e.g. bay-wide in current study — Fig. 1, Table

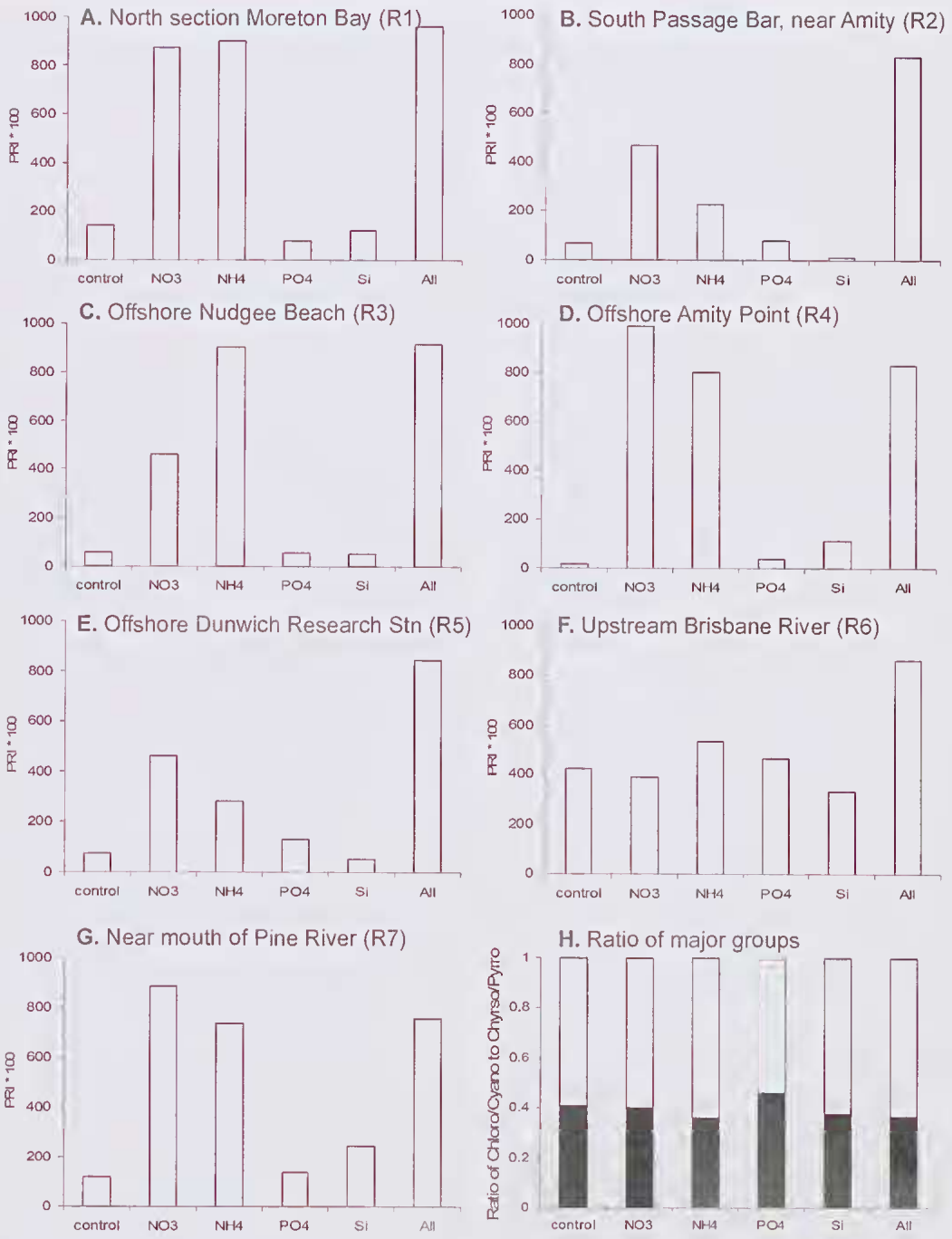

FIG. 4. Resource limitation assays on water samples collected at Sites R1–R7 in Moreton Bay (Fig. 1). Phytoplankton response index (PRI) values were multiplied by 100 (PRI*100) in all cases and plotted against each treatment. The threshold for a significant response was set to 140% greater than the control in order to incorporate errors and temperature effects between assays. (H) Ratios of the major phytoplankton groups did not vary during the course of the assays. In this representative example, we show the ratio of Chlorophyta/Cyanobacteria (Chloro/Cyano) (solid bars) to Chrysophyta/Pyrrophyta (Chryso/Pyrro) (empty bars) after 48 hrs in each of the treatments using water collected at the northern opening of Moreton Bay, R1.

1) versus a focus in southern Moreton Bay and the Logan River in the previous study. From our findings, the southern part of Moreton Bay had lower overall water clarity and phytoplankton communities were N-limited. Both factors would account for lower primary production measurements (0.34 to 0.58 g C m^{-2} day^{-1}) reported by O'Donohue & Dennison (1997). Moreover, our bay-wide results are consistent with average summertime productivity measurements undertaken in other locations in northeastern Australia. Averages recorded for the Gulf of Carpentaria were 0.914 g C m^{-2} day^{-1} (Rothlisberg *et al.* 1994) and 1.33 g C m^{-2} day^{-1} (Motoda *et al.* 1978) while rates in the mid-continental shelf waters off the Great Barrier Reef were 0.55 g C m^{-2} day^{-1} (Furnas & Mitchell 1987). Our findings are also similar to estimates of productivity measured in other temperate and subtropical estuaries further afield, including 0.91 g C m^{-2} day^{-1} in Chesapeake Bay (Harding *et al.* 1986), 0.94 g C m^{-2} day^{-1} in the Neuse River Estuary, USA (Mallin *et al.* 1991) and 0.8 to > 3 g C m^{-2} day^{-1} in temperate Galveston Bay (Quigg *et al.* 2007).

Based on our primary productivity measurements, the Moreton Bay ecosystem was net autotrophic during the period of this study, and generally during Austral summers (Dennison & Abal 1999; Eyre & McKee 2002; Glibert *et al.* 2006). Samples from four sites (Sites 6 & 11 to the west and Sites 9 &14 to the east of the bay had high (25–43) ratios of dark respiration to gross photosynthesis (RR:GPR) compared to other sites sampled (2.9–14.4) (Table 2). Decreases in PAR, sufficient to reduce growth (e.g., due to the highly turbid water column), would impact photosynthesis more than dark respiration. This is consistent with the higher RR:GPR ratios and net growth efficiencies measured landside of the Bay. Although *in situ* PAR is an important factor governing phytoplankton growth (e.g. Quigg & Beardall 2003), and despite a turbidity gradient extending across the Bay, light was not the primary factor controlling phytoplankton productivity during the course of this study.

The combination of oceanic flushing from the east, with riverine nutrient loading from the mainland (west), and the overall clockwise water circulation of the bay establishes a strong nutrient gradient in the bay (Moss *et al.* 1992; Gabric *et al.* 1998; McEwan *et al.* 1998; Glibert *et al.* 2006). Higher productivity rates (net photosynthesis) at sites on the mainland coast of Moreton Bay may be due to nutrient loading from riverine inputs carried north along the mainland by prevailing water currents (Newel 1971; Milford & Church 1977; Patterson & Witt 1992). Bell and Elemetri (2007) reported higher NO_3 levels upstream of the Brisbane River mouth (20.5 µM) compared to the river mouth (14 µM). Low primary production in most sites along the oceanic side of Moreton Bay (Sites 1–5) reflect the influence of oligotrophic waters (Gabric *et al.* 1998; Glibert *et al.* 2006) drawn in by tidal exchange through South Passage. This tidal movement generates strong currents flowing past Dunwich to the south side of Peel I. (Patterson & Witt 1992). Similar cross-bay variation in primary production rates have been reported for other estuaries. For example, in Galveston Bay (Texas, USA), Quigg *et. al.* (2007) recorded summertime high productivity rates of > 3 g C m^{-2} day^{-1} at sites nearest to the Trinity River and 0.8–1.2 g C m^{-2} day^{-1} on the ocean side near the Gulf of Mexico. Similar findings have also been reported for other estuaries including Chesapeake Bay (Harding *et al.* 1986; Malone *et al.* 1988; Fisher *et al.* 1999) and the Strait of Georgia (Harrison *et al.* 1991).

While general trends were observed in water quality and productivity on large spatial scales in Moreton Bay, it is important to appreciate the heterogenous nature of such systems and that exceptions do exist. The sites recording the two highest productivity rates in Moreton Bay, Adam's Beach (Site 14) and the Logan River mouth (Site 13) (Table 2; Fig. 1), are strongly influenced by localized nutrient inputs rather than the general hydrodynamic patterns of the Bay. Despite the presence of oligotrophic oceanic waters in the vicinity, Adam's Beach (Site 14), had the highest net photosynthetic rate (3.9 g C m^{-2} day^{-1}) measured in the study. In the last decade, high phytoplankton productivity along with blooms of the benthic cyanobacterium *Lyngbya majuscula* have been reported at this location (Ahern 2003; Albert *et al.* 2005). These are thought to be fuelled by two nutrient sources. Nutrient-loaded ground water, originating

from the Island's extensive sand dune system, picks up dissolved organic matter (8 mg/L) from nearby *Melaleuca* and *Phragmites* swamps as it travels through sandy substrata before percolating into the supra- and intertidal regions of Adam's Beach (Pointon *et al.* 2003). Effluent, from the outskirts of Dunwich and Adam's Beach caravan parks also ends up at this site (Ahern 2003). The second highest production rate (2.39 g C m^{-2} day^{-1}) was measured in the mouth of the Logan River (Site 13); fueled by urban runoff and the nearby prawn aquaculture facility.

In the majority of resource limitation assays (6 of 7), N as nitrate and/or ammonium limited primary productivity across Moreton Bay (Fig. 4). This is consistent with previous studies by O'Donohue & Dennison (1997) and Glibert *et al.* (2006) which reported summertime N limitation in this estuary. Given the predominant influence of oceanic waters (Fig. 2; Table 1), N-limitation in the Bay is consistent with an oligotrophic environment (Hecky & Kilham 1988; Howarth & Marino 2006). We found no evidence of phosphorus limitation in Moreton Bay, supporting findings of previous studies (O'Donohue & Dennison 1997; Glibert *et al.* 2006) but see Eyre and McKee (2002). Resource limitation bioassays performed on macroalgae and seagrasses, growing in Moreton Bay, also showed preferential responses to N additions (Jones *et al.* 1996; Udy & Dennison 1997) which further raises concerns about the impact of nutrient enrichment in the Bay (Quigg *et al.* 2008).

Although previous studies have reported chlorophyll *a* concentrations in Moreton Bay, this is the first study to our knowledge, using diagnostic photopigments to examine relative abundances of major phytoplankton groups (phylum-level) in the bay. While patterns in phytoplankton biomass distribution (based on chl *a*) were associated with physical and chemical characteristics of the water column, at the phylum level, patterns were less clear. We found Cyanobacteria were a significant component of the phytoplankton pool (Table 1) whereas Wood (1964) and Heil *et al.* (1998 a, b) reported only eukaryotic phytoplankton from Moreton Bay. However Gabric *et al.* (1998) did report the occurrence of *Trichodesmium*, a diazatrophic prokaryotic cyanobacterium in the northern section of Moreton Bay during spring and summer. This pigment approach was not sufficient to provide information on phytoplankton population dynamics and whether the population reflected available resources and/or the physical environment. Using more sensitive techniques for pigment analysis (see Jeffrey *et al.* 1997) and/or microscopic examination of samples may have provided more useful insights into phytoplankton phyla distribution patterns. Assessing phytoplankton population dynamics under a range of resource (e.g., nutrients, light, temperature) conditions would lead to more effective predictive models for Bay protection and identify species which could be used as key bioindicators in defining a healthy estuarine system. Such studies would also identify conditions which can switch either invasive or endemic species into harmful agents (Granéli & Turner 2006). Blooms of the toxin-producing dinoflagellate *Dinophysis caudata*, for example, have been recorded in Moreton Bay from the 1940s and 50s (Wood 1954) and are considered part of the natural cycle. However a change in bloom frequency or occurrence may indicate a perturbation in estuary function. More controversially, there has been an increase in reports of the cyanobacterium *L. majuscula* (which forms dense filamentous mats during the summer months) in Moreton Bay (Bell *et al.* 1999; Elmetri & Bell 2004; Ahern *et al.* 2007), particularly in Deception Bay and near the Port of Brisbane. One of the key factors driving blooms of this species may be its ability to fix nitrogen (Lundgren *et al.* 2003; Elmetri & Bell 2004) so while eukaryotic phytoplankton maybe N-limited during the Austral summer, diazotrophic cyanobacteria such as *L. majuscula* are able to continue growing. Hence the change in *L. majuscula* bloom frequency and magnitude suggests it could be a useful monitoring tool. The occurrence of algal blooms, whether they are considered harmful or simply offensive to humans, has led not only to the loss of wildlife (e.g., fish kills) and flora (e.g., smothering of seagrasses) in Moreton Bay (Dennison & Abal 1999) and other estuaries around the world (Fisher *et al.* 1999; Howarth & Marino 2006; Thronson & Quigg 2008) but also to the loss of revenue e.g. from fewer tourist dollars.

MANAGEMENT IMPLICATIONS

While this study considered the impact of water column quality on phytoplankton productivity in Moreton Bay, future studies should consider nutrient partitioning between the water column, sediment and biota in the Bay. This would provide much needed information to better predict the impact of increased nutrient loading on this coastal ecosystem rather than the generalisations alluded to by the above measurements. For example, based on elemental fluxes, particularly for carbon, nitrogen and phosphorus, Eyre & McKee (2002) concluded that primary productivity was phosphorus limited at the *whole* ecosystem level in Moreton Bay. Our findings indicated that primary productivity was N-limited at the time of the study which was consistent with the conclusions of Moss *et al.* (1992), O'Donohue & Dennison (1997) and Glibert *et al.* (2006). The disparity in these conclusions indicates that we need a better understanding of how nutrient inputs are modified as they move around estuaries by physical, biological and anthropogenic processes, particularly nutrient partitioning and recycling. Such studies can better inform managers of the significance of regulating nutrient loads. While many studies focus on regulating N loading to reduce the impacts of eutrophication (e.g. Rabalais *et al.* 2007) we are becoming increasingly aware of the need to also consider reducing P loads (Eyre & McKee, 2002; Ammerman *et al.* 2003; Elmetri & Bell 2004; Sylvan *et al.* 2007). Irrespective of the source of nutrient-enrichment, our findings support the need for coastal water quality managers to address impacts of nutrient-loading, not only in Moreton Bay, but also in other estuaries.

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LITERATURE CITED

Ahern, K.S. 2003. Effect of nutrients on the cyanobacteria *Lyngbya majuscula*: A bioassay technique. Honours Thesis, University of Queensland.

Ahern, K.S., Ahern, C.R., Savige, G.M. & Udy, J.W. 2007. Mapping the distribution, biomass and tissue nutrient level of a marine benthic cyanobacterial bloom (*Lyngbya majuscula*). *Marine and Freshwater Research* **58**: 883–904.

Albert, S., O'Neil, J.M., Udy, J.W., Ahern, K.S., O'Sullivan, C.M. & Dennison, W.C. 2005. Blooms of the cyanobacterium *Lyngbya majuscula* in coastal Queensland, Australia: disparite sites, common factors. *Marine Pollution Bulletin* **51**: 428–437.

Ammerman, J.W., Hood, R.R., Case, D.A. & Cotner, J.B. 2003. Phosphorus deficiency in the Atlantic: An emerging paradigm in oceanography. *EOS Transactions, American Geophysical Union*. **84**: 165–170.

Bell, P.R.F., Elmetri, I. & Uwins, P. 1999. Nitrogen fixation of *Trichodesmium* spp. in the Great Barrier Reef Lagoon: relative importance of the 'new' nitrogen load. *Marine Ecology Progress Series* **186**: 119–126.

Bell, P.F.R. & Elmetri, I. 2007. Some chemical factors regulating the growth of *Lyngbya majuscula* in Moreton Bay, Australia: importance of sewage discharges. *Hydrobiologia* **592**: 359–371.

Cox, M.E. 1998. Chemical and turbidity character of the tidal Brisbane River, Moreton Bay. Pp. 175–184. *In*, Tibbetts, I.R., Hall, N.J. & Dennison, W.C. (Eds), *Moreton Bay and Catchment*. (School of Marine Science, University of Queensland: Brisbane).

Dennison, W.C. & Abal, E.G. 1999. Moreton Bay Study: A Scientific Basis for the Healthy Waterways Campaign. (South East Queensland Regional Water Quality Management Strategy, Brisbane). 245 pp.

Elmetri, I. & Bell, P.R.F. 2004. Effects of inorganic phosphorus on the growth and nitrogen fixation rates of *Lyngbya majuscula*: potential implications for controlling bloom formation in Moreton Bay, Queensland. *Marine Ecology Progress Series* **281**: 27–35.

Eppley, R.W. 1972. Temperature and phytoplankton growth in the sea. *Fishery Bulletin* **70**: 1063–1085.

Eyre, B.D. & McKee, L. 2002. Carbon, nitrogen and phosphorus budgets for a shallow sub-tropical coastal embayment (Moreton Bay, Australia). *Limnology and Oceanography* **47**: 1043–1055.

Falkowski, P.G., Dubinsky, Z. & Wyman, K. 1985. Growth-irradiance relationships in phytoplankton. *Limnology and Oceanography* **30**: 311–321.

Fisher, T.R., Gustafson, A.B., Sellner, K.R., Lacuture, R., Haas, L.W., Magnien, R., Karrh, R. & Michael,

B. 1999. Spatial and temporal variation in resource limitation in Chesapeake Bay. *Marine Biology* **133**: 763–778.

Furnas, M. & Mitchell, A.W. 1987. Phytoplankton dynamics in the central Great Barrier Reef — II. Primary production. *Continental Shelf Research* **7**: 1049–1062.

Gabric, A.J., McEwan, J. & Bell, P.R.F. 1998. Water quality and phytoplankton dynamics in Moreton Bay, south eastern Queensland. I. Field survey and satellite data. *Marine and Freshwater Research* **49**: 215–225.

Glibert, P.M., Conley, D.J., Fisher, T.R., Harding, L.W. & Malone, T.C. 1995. Dynamics of the 1990 winter/spring bloom in Chesapeake Bay. *Marine Ecology Progress Series* **122**: 27–43.

Glibert, P.M., Heil, C.A., O'Neil, J.M, Dennison, W.C. & O'Donohue, M.J.H. 2006. Nitrogen, phosphorus, silica, and carbon in Moreton Bay, Queensland, Australia. Differential limitation of phytoplankton biomass and production. *Estuaries and Coasts* **29**: 209–221.

Granéli, E. & Turner, J.T. 2006. *Ecology of Harmful Algae*. Ecological Studies Vol. 189. (Springer Verlag: Heidelberg) 413 pp.

Hambrook-Berkman, J.A. & Canova, M.G., 2007. Algal biomass indicators (ver. 1.0): U.S. Geological Survey Techniques of Water-Resources Investigations, Book 9, Chap. A7, Section 7.4, online: http://pubs.water.usgs.gov/twri9A/

Harding, L.W., Meeson, B.W. & Fisher, T.R. 1986. Phytoplankton production in two East Coast estuaries: Photosynthesis-light functions and patterns of carbon assimilation in Chesapeake and Delaware Bays. *Estuarine, Coastal and Shelf Science* **23**: 773–806.

Harrison, P.J., Clifford, P.J., Cochlan, W.P., Yin, K., St. John, M.A., Thompson, P.A., Sibbald, M.J. & Albright, L.J. 1991. Nutrient and plankton dynamics in the Fraser River plume, Strait of Georgia, British Columbia. *Marine Ecology Progress Series* **70**: 291–304.

Hecky, R.E. & Kilham, P. 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: A review of recent evidence on the effects of enrichment. *Limnology and Oceanography* **33**: 796–822.

Heil, C.A., O'Donohue, M.J. & Dennison, W.C. 1998a. Aspects of the winter phytoplankton community of Moreton Bay. Pp. 291–300. *In*, Tibbetts, I.R., Hall, N.J. & Dennison,W.C. (Eds), *Moreton Bay and Catchment*. (School of Marine Science, University of Queensland: Brisbane).

Heil, C.A., O'Donohue, M.J., Miller, C.A. & Dennison, W.C. 1998b. Phytoplankton response to a flood event. Pp. 569–584. *In*, Tibbetts, I.R., Hall, N.J. & Dennison,W.C. (Eds), *Moreton Bay and Catchment*. (School of Marine Science, University of Queensland: Brisbane).

Howarth, R.W. 1988. Nutrient limitation of net primary production in marine ecosystems. *Annual Review of Ecology and Systematics* **19**: 89–110.

Howarth, R.W. & Marino, R. 2006. Nitrogen as the limiting nutrient for eutrophication in coastal marine ecosystems: Evolving views over 3 decades. *Limnology and Oceanography* **51**: 364–376.

Jeffrey, S.W., Mantoura, R.F.C. & Wright, S.W. 1997. Phytoplankton pigments in oceanography: guidelines to modern methods. *Monographs on oceanographic methodology*. (UNESCO Publishing: France) 661 pp.

Jones, A., Dennison, W.C. & Stewart, G.R. 1996. Macroalgal responses to nitrogen source and availability: Amino acid metabolic profiling as a bioindicator using *Gracilaria edulis* (Rhodophyta). *Journal of Phycology* **32**: 757–766.

Laws, E.A. 1991. Photosynthetic quotients, new production and net community production in the open ocean. *Deep-Sea Research* **38**: 143–167.

Lundgren, P., Bauer, K., Lugomela, C., Soderback, E. & Bergman, B. 2003. Re-evaluation of the nitrogen fixation behaviour in the marine non-heterocystous cyanobacterium *Lyngbya majuscula*. *Journal of Phycology* **39**: 310–314.

MacKinney, G. 1941. Absorption of light by chlorophyll solutions. *Journal of Biological Chemistry* **140**: 315–322.

Mallin, M.A., Paerl, H.W. & Rudek, J. 1991. Seasonal phytoplankton composition, productivity and biomass in the Neuse River estuary, North Carolina. *Estuarine, Coastal and Shelf Science* **32**: 609–623.

Malone, T.C., Crocker, L.H., Pike, S.E. & Wendler, B.W. 1988. Influences of river flow on the dynamics of phytoplankton production in a partially stratified estuary. *Marine Ecology Progress Series* **48**: 235–249.

McEwan, J., Gabric, A.J. & Bell, P.R.F. 1998. Water quality and phytoplankton dynamics in Moreton Bay, south-eastern Queensland. II. Mathematical modelling. *Marine and Freshwater Research* **49**: 227–239.

Milford, S.N. & Church, J.A. 1977. Simplified circulation and mixing models of Moreton Bay, Queensland. *Australian Journal of Marine and Freshwater Research* **28**: 23–34.

Moss, A., Connell, D.W. & Bycroft, B. 1992. Water quality in Moreton Bay. Pp. 103–113. *In*, Crimp, O. (Ed.), *Moreton Bay in the Balance*. (Australian Littoral Society & Australian Marine Science Consortium: Brisbane).

Motoda, S., Kawamura, T. & Taniguchi, A. 1978. Differences in productivities between the Great Australian Bight and the Gulf of Carpentaria, Australia, in summer. *Marine Biology* **46**: 93–99.

Newell, B.S. 1971. The hydrological environment of Moreton Bay, Queensland 1967–68. CSIRO Division of Fisheries and Oceanography Technical Paper No 30.

O'Donohue, M.J.H. & Dennison, W.C. 1997. Phytoplankton productivity response to nutrient concentrations, light availability and temperature along an Australian estuarine gradient. *Estuaries* **20**: 521–533.

Patterson, D. & Witt, D. 1992. Hydraulic processes in Moreton Bay. Pp. 25–39. *In*, Crimp, O. (Ed.), *Moreton Bay in the Balance*. (Australian Littoral Society & Australian Marine Science Consortium: Brisbane).

Phillips, J.A. & Kevekordes, K. 2008. An evaluation of the role of macroalgae in mangrove dieback at Whyte Island, Moreton Bay, subtropical eastern Australia. In: Davie, P.J.F. & Phillips, J.A (Eds) Proceedings of the Thirteenth International Marine Biological Workshop on the Marine Fauna and Flora of Moreton Bay, Queensland. Volume 1. *Memoirs of the Queensland Museum Nature* **54** (1): 405–419.

Pointon, S.M., Moody, P.W., Preda, M., Cox, M., Hey, K., Ahern, C.R. & Powell, B. 2003. Investigation of terrestrial sources of nutrients supporting *Lyngbya majuscula* growth in Moreton Bay – Land Sources. (Department of Natural Resources and Mines: Indooroopilly, Queensland, Australia).

Quigg, A. & Beardall, J. 2003. Protein turnover in relation to maintenance metabolism at low photon flux in two marine microalgae. *Plant, Cell and Environment* **26**: 1–10.

Quigg, A. & Roehrborn, L. 2008. Spatial and temporal distributions of planktonic diatoms in a subtropical bayou. *Texas Journal of Science*. **60**: 281–298.

Quigg, A., Davis, S.E. & Roelke, D.F. 2007. Changes in freshwater inflows and how they effect Texas Bays. Final Report of the Coastal Coordination Council pursuant to National Oceanic and Atmospheric Administration Award No. NA05NOS4191064. pp. 47.

Quigg, A., Kevekordes, K. & Phillips, J.A. 2008. Ecophysiological status of nine species of macroalgae and seagrasses in Moreton Bay, Queensland, Australia. *In*, Davie, P.J.F. & Phillips, J.A. (Eds), Proceedings of the Thirteenth International Marine Biological Workshop, The Marine Fauna and Flora of Moreton Bay, Queensland. *Memoirs of the Queensland Museum Nature* **54** (1): 391–403.

Rabalais, N.N., Turner, R.E., Sen Gupta, B.K., Boesch, D.F., Chapman, P. & Murrell, M.C. 2007. Characterization and long-term trends of hypoxia in the Northern Gulf of Mexico: Does the science support the action plan? *Estuaries and Coasts* **30**: 753–772.

Rhee, G.-Y. 1980. Continuous culture in phytoplankton ecology. *Advanced Aquatic Microbiology* **2**: 151–194.

Rothlisberg, C., Pollard, P.C., Nichols, P.D., Moriarity, D.J.W., Forbes, A.M.G., Jackson, C.J. & Vaudrey, D. 1994. Phytoplankton community structure and productivity in relation to the hydrological regime of the Gulf of Carpentaria, Australia, in summer. *Australian Journal of Marine and Freshwater Research* **45**: 265–282.

SCOR-UNESCO 1966. *Determination of photosynthetic pigments in seawater. Monographs on Oceanographic Methodology* **1**: 11–18. (UNESCO: Paris).

Steele, J. 1990. Tides, currents and dispersion. Pp. 63–70. *In*, Davie, P., Stock, E. & Low Choy, D. (Eds), The Brisbane River. (Australian Littoral Society & Queensland Museum: Brisbane).

Strickland, J.D.H. & Parsons, T.R. 1972. A practical handbook of sea-water analysis. (2nd Edition). (Bulletin of the Fisheries Research Board Canada, No 167: Ottawa) 311 pp.

Sylvan, J.B., Quigg, A., Tozzi, S. & Ammerman, J.W. 2007. Eutrophication induced phosphorus limitation in the Mississippi River Plume: Evidence from fast repetition rate fluorometry. *Limnology and Oceanography* **52**: 2679–2685.

Thronson, A. & Quigg, A. 2008. Fifty five years of fish kills in Coastal Texas. *Estuaries and Coasts* **31**: 802–813.

Udy, J.W. & Dennison, W.C. 1997. Growth and physiological responses of three seagrass species to elevated sediment nutrients in Moreton Bay, Australia. *Journal of Experimental Marine Biology and Ecology* **217**: 253–277.

Verity, P.G. 1982. Effects of temperature, irradiance, and daylength on the marine diatom *Leptocylindrus danicus* Cleve. III. Dark respiration. *Journal of Experimental Marine Biology and Ecology* **60**: 197–207.

Wetzel, R.G. & Likens, G.E. 2000. *Limnological Analyses*. Third Edition. (Springer: New York). 429 pp.

Wood, E.J.F. 1954. Dinoflagellates in the Australian region. *Australian Journal of Marine and Freshwater Research* **5**: 171–352.

1964. Studies on the microbial ecology of the Australasian region. V. Microbiology of some Australian estuaries. *Nova Hedwigia* **8**: 461–527.